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The structure of the littoral: effects of waterlily density and perch predation on sediment and plant-associated macroinvertebrate communities

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SUMMARY

1. Littoral zones are complex and important for mechanisms that maintain clear water and submerged plant dominance in lakes. Details of their structure are scarce, largely because sweep or grab sampling, the most commonly used approach, is unable to reveal much subtlety.
2. Invertebrate communities of plankton and sedimentary benthos, and of those living on submerged and floating leaves and their petioles of *Nuphar lutea*, were separately sampled from 2-m^2 mesocosms in a shallow lake, with different lily densities in the absence or presence of perch (*Perca fluviatilis*).
3. Increasing plant density led to reduced sedimentary benthos populations other than those of tubificids. This was ascribed to greater shading of algal producers on the surface sediment by the increasing leaf canopy.
4. Increasing leaf canopy increased the populations of several plant-associated taxa, suggesting that habitat availability was potentially limiting for these.
5. Submerged leaves supported more invertebrates per unit area than submerged petioles or the undersides of floating leaves. Greater periphyton production on leaf surfaces that had thinner cuticles and less waxy surfaces was probably responsible.
6. Perch predation had unexpectedly little effect, although the perch fed widely among the subhabitats, and fish population densities were relatively high. Predation was most intense on the planktonic and sedimentary benthos communities, especially on actively motile invertebrates such as isopods and amphipods. Macroinvertebrates associated with plant surfaces, not least the predominant *Acroloxus lacustris*, were relatively immune. There were more predator effects on submerged leaves than on floating leaves and their petioles.
7. Perch fed less effectively on some taxa at naturally high plant densities than at low and medium densities, and overall, the littoral communities showed resilience to fish predation, probably through the complexity of the plant structure.

Keywords: epiphytic fauna, mesocosms, *Nuphar lutea*, shallow lake

Introduction

Plant-dominated littoral zones dominate the productivity (Wetzel, 1964; Wetzel & Hough, 1973) of shallow lakes that have not become unduly eutrophicated (when the littoral may be reduced to the bottom area under only a few centimetres of water by the shading effects of large phytoplankton populations). They bear communities of micro- and macroalgae and vascular plants that give a structure to the littoral zone that is much more complex (Carpenter & Lodge, 1986) than that of the plankton in the open water. Their large concentration of biomass means that metabolically they are very active and their shallowness and proximity to the land mean that nutrient

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supplies are more plentiful than at the centre of the lake. Their sediments tend to be more organic, the mixing effects of water movements less active (in summer at least) and their biodiversity much higher than towards the centre of the lake. Not least, they contain several subcommunities of invertebrates (Macan, 1974), associated with the bottom sediments, the vegetation, the interstitial water among the plants and the surface film. Sediments and planktonic habitats are also present in the deeper water, but wind mixing and sediment sorting tends to reduce them to greater simplicity.

Most attention, in the littoral zone, has been paid to the macrophyte communities, with their inclusion of thalloid and filamentous algae (Cantonati & Lowe, 2014), and submerged, floating and floating-leaved plants, melding with emergent reed swamp plants and the wetland communities of the hinterland. Studies have documented the roles of the plant communities in influencing the whole lake through nutrient and organic matter transfers (Schindler & Scheuerell, 2002), and provision of cover or refuges for fish and zooplankters (Timms & Moss, 1984; Carpenter & Lodge, 1986). The consequences of loss of macrophytes have been well documented, and much research has considered the conditions needed for reinstatement of macrophyte communities that have been lost (e.g. Moss, 1995). Littoral zone ecology has also stimulated much work on the theoretical ecology of changing or alternative states (e.g. Uhlmann, 1980; Irvine, Moss & Balls, 1989; Scheffer *et al*., 1993, 2001, 2009).

The animal communities, other than those of small zooplanktonic crustacea that may migrate into the open water, have received less attention, despite their richness and despite a suggestion that the plants provide refuges not only for zooplankters but also for grazers on periphyton that would otherwise reduce plant growth (Phillips, Eminson & Moss, 1978) and therefore contribute a buffer mechanism to maintain a plant-dominated state (Moss, Madgwick & Phillips, 1996). Interest in the invertebrate communities has waned except for studies linked with predator–prey and niche breadth theory. Typically, where they are studied, the invertebrate communities are mass-sampled by sweep nets, grabs and dredges that remove a jumbled mass of plants, mud, water and animals that loses all of its previous structure.

As a result, although the complexity of the littoral is often trumpeted, there are relatively few details of it. This study, following earlier work (Hall, Cooper & Werner, 1970; Kajak, 1970; Macan, 1973; Werner *et al*., 1983; Tolonen *et al*., 2001), dissects some of the spatial relationships among the littoral invertebrate communities within the lily beds of a shallow lake, using experimental mesocosms in which the plant density and influence of fish predation were manipulated to create six different habitat structures. It was carried out in Little Mere in north-west England, where a pioneering study (Barker, Irfanullah & Moss, 2010) on the diurnal changes of chemistry and plankton communities within the lily beds showed a fine structure that changed diurnally and was undetectable by conventional water sampling. In the present work, the macroinvertebrate communities in the water, associated with the submerged and floating leaves and their petioles, of the yellow water lily, *Nuphar lutea*, and in the bottom sediments, were separately sampled and measured. The results from studies on the plankton within the mesocosms have already been published (Moss, Kornijów & Measey, 1998). The present article is largely concerned with the benthic and plant-associated communities and integrates results from the plankton.

Macroinvertebrates in habitats colonised by water lilies have been seldom studied, and generally in separate studies of the sedimentary benthos (Kornijów & Moss, 1997; Żbikowski, Kobak & Żbikowska, 2010) or epiphyton associated with plant surfaces (McGaha, 1952; Brock & van der Velde, 1996; Dvorak, 1996; Cronin, Wissing & Lodge, 1998; Kornijów & Ścibior, 1999; Nurminen *et al*., 2010b; Da Silva, Albertoni & Palma-Siva, 2015). The role of fish in structuring the sedimentary benthos and plant-associated communities together has been rarely examined (Schramm & Jirka, 1989; Kornijów *et al*., 2005), compared with work on combined grab samples and on the plankton. Some invertebrate taxa live both in sediment and on plant surfaces (Diehl & Kornijów, 1998). If only macroinvertebrates associated with vegetation or with sediment are sampled, the effects of fish predation cannot be distinguished from simple migration among the different substrata.

Our overall aim was to establish the degree to which these invertebrate communities are influenced by habitat availability and fish predation, and five specific hypotheses were tested. These were as follows:

1. that plant-associated invertebrate communities are limited by habitat availability so that provision of greater plant biomass would result in larger numbers or biomass of invertebrates on a per unit area of habitat basis;

2. that different qualities of leaf surface (thin, flexible submerged leaves compared with the undersides of more rigid, floating blades with thicker cuticles, and with the petioles of the latter), would result in different communities, with greater numbers and biomass of

grazers of epiphytic periphyton on the submerged leaves;

3. that feeding by a generalist fish predator, young common perch (*Perca fluviatilis*), 2–3 years old, which were the most abundant fishes in the lake, would show selective predation resulting in reduction in numbers of motile, more easily detectable macroinvertebrates, such as insects and crustaceans, compared with sedimentary or slow-moving ones, such as gastropods or case formers;

4. that greater provision of macrophyte biomass would result in greater numbers and biomass of benthic invertebrates through greater supply of organic matter to the bottom sediments; and

5. that fish feeding would be hampered with increasing complexity of the vegetation.

Methods

Eighteen experimental enclosures (1 × 2 m) were built in a dense and uniform bed of *N. lutea* in Little Mere, north-western England (53°20′N, 2°24′W; area: 2.5 ha, max. depth: 1.7 m). For more details on the lake, see Moss *et al.* (1997, 2005). The enclosures were of curtain netting (mesh size: <50 μm) fixed onto a wooden framework, pushed into the sediment in about 75 cm of water. The lake bottom consisted of organic-rich sediments covered by 20–25 cm loose organic ooze. Three densities of floating leaves were established by leaving the stand intact in six enclosures (high density), cutting about half of the leaves in a further six (medium) and cutting between three-quarters and two-thirds of the leaves in the remaining six (low). The remaining leaves covered about 90, 50 and 25% of the water surface, respectively. The surviving leaves were marked with a waterproof marker and any new floating leaves, except as needed to replace those that had died, were cut as they were initiated, during the experiment, which ran from 10 June until 8 August 1993. Submerged leaves were allowed to grow, so as to minimise disturbance, but were lesser contributors.

After the plant densities had been established, and fish had been removed by repeated electrofishing, the enclosures were allowed to stabilise for 1 week, prior to use. On 16 June 1993, six perch (mean length: 14.8 cm, SD: 0.8 cm) were added to each of the three enclosures at each plant density. Three enclosures at each plant density remained fishless. All enclosures were covered by 2 cm × 2 cm thin plastic netting to prevent predation by birds. Light penetration was negligibly affected. There were thus six treatments: low, medium and high plant density without fish, and low, medium and high plant density with fish, each replicated three times, with treatments randomised among the enclosures. To simulate progressive decline of this juvenile perch population during the summer, two fish from each fish enclosure were removed in the middle of the experiment. The enclosures were inspected every second or third day, and dead fish were replaced with individuals of a similar size. The overall mortality of the fish was 12%. All of the fish used in the experiment were collected by seining in Little Mere. At the end of the experiment, vegetation was harvested and all fish removed from the enclosures with a net constructed from 8-mm mesh material attached to a wooden frame, which fit snugly inside the enclosures. Each enclosure was netted repeatedly until no more fish were collected in at least three successive hauls. The fish were dissected, and their stomach contents were preserved with 4% formaldehyde solution and then examined under a dissecting microscope.

Sedimentary benthic macroinvertebrates were sampled from within the enclosures three times: at the start of the experiment (June 16), on July 13 and at the end of the experiment (August 10). Samples were collected using a perspex tube (cross-sectional area: 15 cm^2, length: 120 cm). One sample comprised of six sediment cores, 10 cm deep, pooled together. Three such samples were collected from each enclosure on each occasion. The number of subsamples, and the sediment depth taken into account, was based on pilot sampling to determine depth of burrowing of the animals. The sample was sieved through a 400-m mesh net. Invertebrates were sorted by eye and preserved in 4% formaldehyde. After blotting, the formalin wet biomass of all organisms in each taxon was determined to a precision of ±0.1 mg.

Plant-associated fauna was collected in August at the end of the experiment because it involved destructive sampling. Firstly, randomly chosen floating leaf blades were cut at their junctions with their petioles and sampled for their animals by means of a trap sampler (Kornijów, 1998). The sampler (trapping area: 154 cm^2, length: 32 cm) consisted of two halves of a perspex tube (cut lengthwise) joined at one edge with hinges and having openings covered with 220-μm mesh netting. Then, the invertebrates dwelling on petioles of the floating leaves were sampled using another core sampler, equipped with a 220-μm sieve (Kornijów & Kairesalo, 1994). A length of petiole was enclosed by the sampler and then cut at both ends with scissors. One sample consisted of 3–4 leaves or petioles. Macrofauna associated with blades of submerged leaves was sampled in the same way as that for floating leaf blades. However,

the petioles were not separately sampled because of their shortness and small surface area. From each enclosure, three samples of floating and three samples of submerged leaves (with the exceptions of enclosures 5 and 15, where the final number of the leaves accommodated only two) were taken. Animals were sorted and preserved in formalin, counted and weighed.

The surface areas of the collected petioles of the floating leaves were measured directly, whilst those of the blades of floating leaves (y_f) and submerged leaves (y_s) were derived from the regression equations of surface area and dry mass of the leaves, where x = dry weight of leaves and surface areas are given in cm^2: $y_f = 95.3x + 72.3$ ($r^2 = 0.909$, $P < 0.0001$, $n = 30$); $y_s = 556x - 2.04$ ($r^2 = 0.803$, $P < 0.001$, $n = 30$). The equations are based on measurements of the surface areas of randomly chosen leaf blades made with an automatic area meter (Hayashi Denko Co. Ltd, Bunkyo-ku, Japan). The desired conditions of plant cover were achieved (Fig. 1), with a significant gradient in total plant cover, determined largely by the floating leaves and their petioles. Submerged plant cover was not significantly different in the three plant treatments, but the presence of fish reduced it by 38%.

At the end of the experiment, one of the low plant density with fish enclosures was found to have in it a single tench (*Tinca tinca*). Although inclusion of data from this enclosure made little difference to the conclusions, the data were excluded from the analyses. After fish stomach contents had been identified and counted, Renkonen similarity indices (Renkonen, 1938) were calculated to determine the similarity (as %) of stomach contents with the composition of the communities in the sediments and on the component parts of the water lilies. The index is as follows: $S_r = \sum \min(p_1 \ldots p_i)$, where p is the lower of the percentages in the total sample and in the fish guts for each taxon shared between the fish gut and the habitat. Manly, Miller & Cook's (1972) electivity index, assuming no food limitation (Chesson, 1978), was also calculated based on the gut contents and the overall community (sedimentary benthos, planktonic and plant-associated animals) composition. The index is as follows: $\alpha = r_i/n_i$ ($\sum r/n$), where r is the proportion of species in the guts and n is the proportion in the available prey community. It is calculated separately for each species i.

Temperature and dissolved oxygen concentration were measured with a thermistor and oxygen probe once in a fortnight, just below the surface and just above the bottom in each of the enclosures, but showed no significant differences among the treatments or among the replicates. There was a distinct temperature gradient between the surface and bottom by day, which was less marked but still persistent at night. The oxygen gradient was stronger; it intensified in the afternoon and was greatest at night. Values at the bottom fell to zero in some cases by 03:00 hours. Detailed data on these variables are given in Kornijów & Moss (1997, 2003).

Results for sedimentary benthos were analysed by repeated-measures analysis of variance. Results for plant-associated invertebrates were analysed by two-way analysis of variance. Tukey's tests were used to determine *post hoc* any differences among the plant treatments. Pearson's correlation coefficients were calculated to relate communities on different plant structures. SPSS version 22 (IBM United Kingdom Limited, Hampshire, England) was used for statistical calculations.

Results

Composition of the fauna

Figure 2 shows the proportions of the main taxa found on different substrata and divides them among feeding guilds. Table S1 shows the full list of macroinvertebrates recorded, with a measure of their relative density per

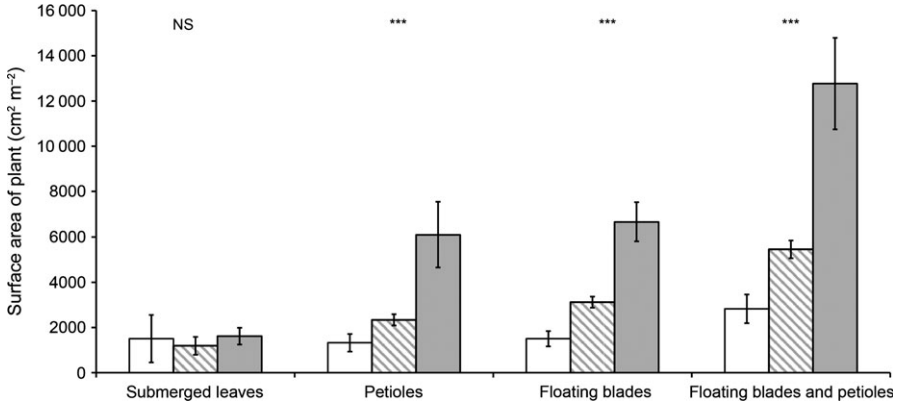

Fig. 1 Differences in plant community (surface area in cm^2 m^{-2} of bottom) in different treatments. Values are means ± standard deviation. White bars are low; hatched bars, medium; and grey bars, high plant densities. The probability for submerged leaves was 0.06, much less significant than the values of <0.0001 shown as *** for other entities.

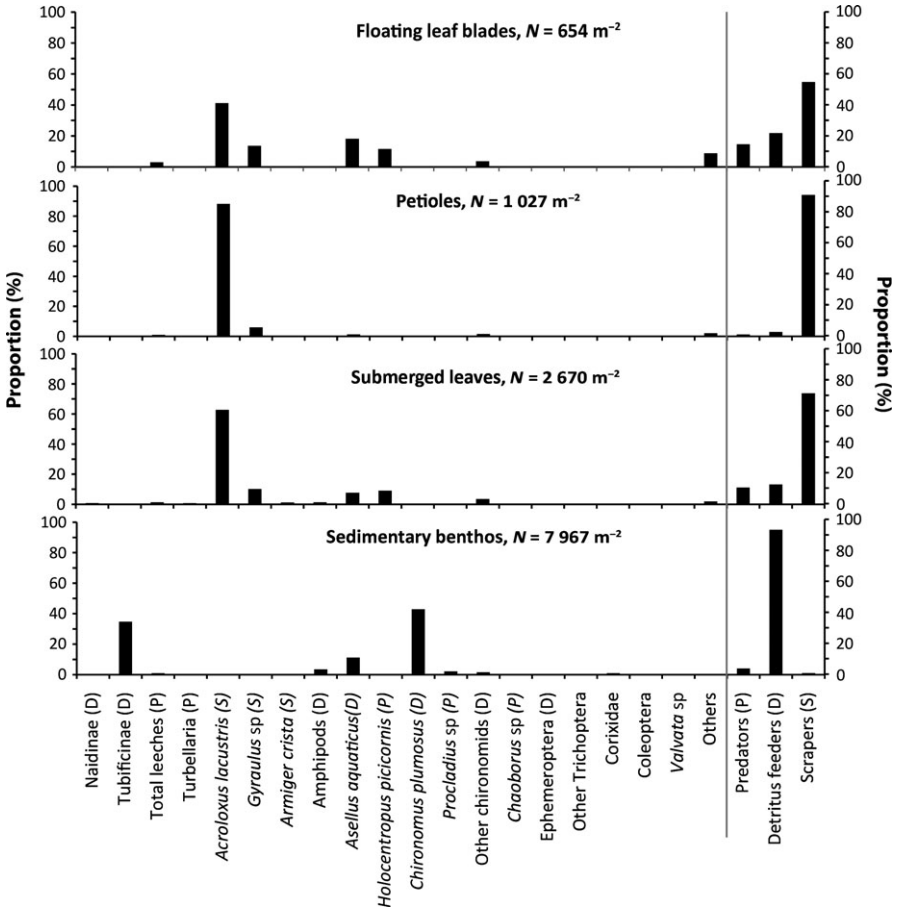

Fig. 2 Composition of the benthic and plant-associated communities by major taxa and feeding guilds, based on the samples taken in August. Numbers are percentages of the total sample and are means of the samples taken over all treatments. S, scraper; D, detritivore/herbivore; P, predator.

unit area of substratum (sediment for benthos, leaf surface for plant-associated taxa). The habitats were about equally species-rich, with a few more taxa on the undersides of floating leaf blades. Total densities were larger for the benthos but mostly because of an abundance of burrowing oligochaetes (Tubificidae). Beyond these, *Asellus aquaticus*, *Crangonyx pseudogracilis*, *Chironomus* f.l. *plumosus* and *Procladius* sp. dominated a community in which chironomid diversity was high. *Asellus aquaticus*, *Holocentropus picicornis* and *Acroloxus lacustris* dominated the plant-associated community in which periphyton scrapers, as opposed to deposit feeders, were most prominent. Ten taxa were confined to the benthos, 19 were confined to the plant surfaces, and 13 were shared. There was considerable distinction between the communities but with *A. aquaticus*, in particular, shared among them.

There were relatively few large invertebrate predators (odonates, beetles, bugs) recorded. It is possible that this was because they may have escaped the sampling methods used, although this is unlikely where the sedimentary benthos is concerned because sampling was very intensive. We could not use sweep nets, commonly used to catch fast-moving predators among plants, as these would have destroyed the structure of the experiment, but the water quality in the lake is likely to have mitigated against large numbers of these. The lake was recovering from sewage effluent discharge, diverted 2 years previously, and its oxygen concentrations were relatively low.

Changes in sedimentary benthos

Increasing plant density resulted in declines in numbers of benthic invertebrates (Table 1) for all those taxa showing significant changes, but tubificids were unaffected. Perch reduced the numbers of the most motile macroinvertebrates (crustaceans and corixids) but not of burrowing species. Some taxa declined with time, largely larvae of insects, perhaps through emergence, but also the leech, *Helobdella* sp., whilst valvatids, amphipods and tubificids increased. Overall, there was no significant change in total numbers, increase in one group compensating for decline in another. The trend for declining numbers of animals with increasing plant cover was seen also for biomass (Fig. 3, Table S2) with

Table 1 Influence of overlying lily density, presence or absence of perch and date of sampling on numbers of sedimentary benthos

Plants	Low plant density (N = 54)	Medium plant density (N = 54)	High plant density (N = 54)	P (main)	P (plants × time)
All macroinvertebrates	8044 ± 4611 a	9863 ± 4989 a	6724 ± 5348 b	**0.004**	0.32 NS
All chironomids	5072 ± 2992 a	5534 ± 2928 b	3798 ± 2318 c	**<0.0001**	0.83 NS
Chironomus plumosus	4622 ± 2764 a	5199 ± 2925 b	3247 ± 1772 c	**<0.0001**	0.89 NS
Procladius sp.	230 ± 243 a	236 ± 249 a	108 ± 172 b	**0.003**	**0.011**
Chironomids other than *C. plumosus*	437 ± 479 a	335 ± 322 a	118 ± 182 b	**<0.0001**	**0.026**
Corixids	75.2 ± 124 a	94 ± 161 a	32.0 ± 77.2 b	**0.022**	0.22 NS
Asellus aquaticus	876 ± 1052 a	628 ± 612 ab	480 ± 562 b	**0.015**	**0.004**
Tubificids	1555 ± 2196	2921 ± 3531	2361 ± 4132	0.11 NS	0.30 NS

Fish	No fish (N = 81)	Fish (N = 81)	P (main)	P (plants × fish)	P (fish × time)
All macroinvertebrates	8312 ± 5220	8110 ± 5066	0.78 NS	**0.006**	0.78 NS
All chironomids	4815 ± 3249	4417 ± 2627	0.28 NS	**<0.0001**	0.83 NS
C. plumosus	4556 ± 3083	4074 ± 2517	0.17 NS	**<0.0001**	0.77 NS
Procladius sp.	164 ± 207	220 ± 250	0.104 NS	**0.013**	0.80 NS
Chironomids other than *C. plumosus*	258 ± 410	335 ± 325	0.14 NS	0.52 NS	0.43 NS
Corixids	98.0 ± 141	34.9 ± 103	**0.001**	0.17 NS	NS (0.08)
A. aquaticus	854 ± 851	463 ± 659	**0.001**	0.11 NS	**0.005**
Amphipods	163 ± 336	30 ± 73	**<0.0001**	0.16 NS	**<0.0001**
Tubificids	1893 ± 2676	2678 ± 4008	0.13 NS	0.36 NS	0.13 NS

Date	June (N = 54)	July (N = 54)	August (N = 54)	P (main)
All macroinvertebrates	9193 ± 4149	7891 ± 5602	7538 ± 5454	0.18 NS
All chironomids	6519 ± 3399 a	3798 ± 2318 bc	3515 ± 1978 c	**<0.0001**
C. plumosus total	6185 ± 3228 a	3500 ± 2253 bc	3247 ± 1772 c	**<0.0001**
Procladius sp.	169 ± 201	244 ± 259	160 ± 222	(0.095) NS
Chironomids other than *C. plumosus*	335 ± 474	296 ± 318	256 ± 298	0.53 NS
Chaoborus sp.	83.7 ± 125 a	19.7 ± 60.1 bc	35.1 ± 83.1 c	**0.001**
Corixids	106 ± 149 a	29.6 ± 76.1 b	65.3 ± 135 ab	**0.004**
A. aquaticus	527 ± 359	658 ± 807	798 ± 1030	NS
Amphipods	62 ± 99 a	34.5 ± 93.8 a	197 ± 398 c	**<0.0001**
Coleoptera	78.8 ± 138 a	4.9 ± 25.3 b	5.0 ± 25.6 bc	**<0.0001**
Valvatids	2.51 ± 18.3 a	12.3 ± 46.7 a	37.6 ± 75.5 b	**0.002**
Helobdella sp.	251 ± 317 a	86 ± 119 b	67.5 ± 118 bc	**<0.0001**
Tubificids	1229 ± 1592 a	2953 ± 3873 b	2675 ± 4070 ab	**0.016**

Values are numbers m^{-2} and are means ± standard deviation. Values sharing a letter along rows are not significantly different at $P < 0.05$. Only taxa showing at least a significant difference in main effect and taxa that were otherwise particularly abundant are shown. Values highlighted in bold in this and subsequent tables are significant to at least $P = 0.05$.

chironomids and total biomass also showing a decrease in the presence of fish, although the effect sizes were small. There were few interaction effects (Table 1) between plant treatment and time or between fish and plant treatments. Among the latter (Fig. 4), fish effects of reducing biomass at low and medium plant densities were reversed for total macroinvertebrates and for total chironomids at high plant densities or severely muted for mobile animals such as *A. aquaticus* and total amphipods.

Changes in density of plant-associated macroinvertebrates per unit area of plant surface

The submerged leaves and the floating leaves (and their petioles) provided different substrata for animal colonisation. Very few taxa were confined to submerged leaves or to floating leaves and their petioles, but there were notable differences in relative abundance. Density of macroinvertebrates per unit area of leaf was very strongly correlated among mesocosms between submerged leaves and floating leaf blades and strongly correlated between petioles and floating leaf blades (Fig. 5). About four times as many animals were found per unit area on submerged leaves (267 ± 11.3) than on floating leaves (65.4 ± 21.7) (reduced to twice when allowance is made for the two-sided availability on submerged leaves but only one side in floating leaves). There were 2.6 times as many on submerged leaves than on petioles (102.7 ± 30.2) and 1.6 times more on petioles than on floating leaf blades. Differences were significant (one-way ANOVA at

$P < 0.03$). *A. lacustris*, *Gyraulus* sp., *A. aquaticus* and *H. picicornis* were all significantly more abundant (one-way ANOVA $P < 0.001$) on submerged leaves than on floating leaf blades or their petioles.

There were few effects of plant density treatment on the numbers per unit area of plant surface (Table 2), and even when there were significant differences, they did not fall into a consistent pattern. The epiphytic *A. lacustris*, which dominated the communities, and the total numbers of macroinvertebrates, were unaffected on submerged plants, declined with plant cover on floating blades and formed a pattern with a maximum at medium plant coverage on the petioles. The next most abundant animal, a snail, *Gyraulus* sp., however, consistently decreased with plant cover, whilst *H. picicornis* increased slightly. *Asellus aquaticus* tended to decrease but mainly on the floating blades. There were different patterns specific to the size classes of this animal on submerged leaves and petioles. The presence of fish (Table 3) caused relatively few changes, with *A. lacustris* again not affected and *Gyraulus* tending to increase in the presence of fish. *Asellus aquaticus* showed irregular patterns but, with chironomids, tended to increase in numerical density a little in the presence of fish. Fish caused reductions in density in none of the taxa, and there were no significant changes in total numbers of macroinvertebrates. Interaction effects between plant density and fish were very few and showed no particular pattern.

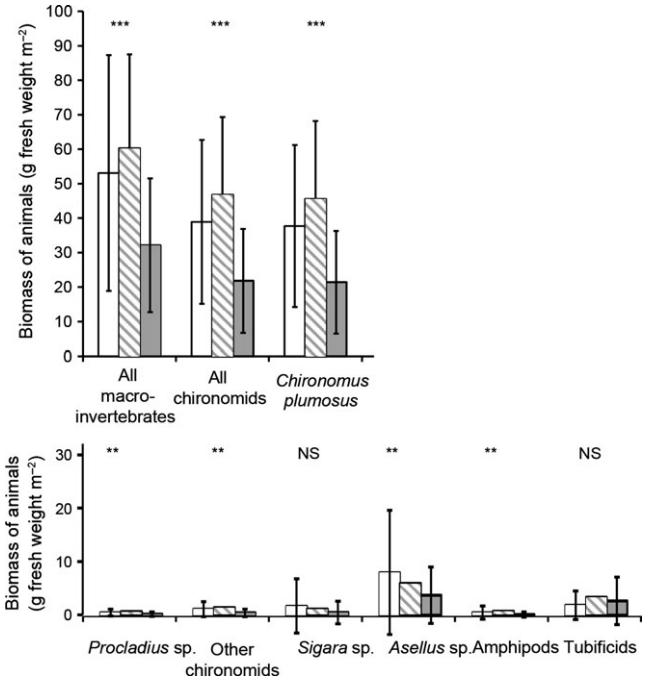

Fig. 3 Influence of overlying lily density on biomass of sediment benthos. Values are g fresh weight m^{-2} and are means ± standard deviation. White bars are low; hatched bars, medium; and grey bars, high plant densities. Data are given only for those taxa showing significant difference in main effect and for those otherwise that were particularly abundant. $^{**}P < 0.001$; $^{***}P < 0.0001$.

Changes in density of plant-associated animals per unit area of habitat

There is an additional dimension to invertebrate abundance where plants are concerned. Not only is there a density per unit area of leaf, reported above, but also, because of the layering of leaves within the water column (the leaf area index, LAI) an abundance in relation to bottom habitat area. Table 4 shows the influence of increasing LAI, reflected in the low, medium and high plant treatments, on invertebrate abundance. The expectation would be that increasing LAI would lead to

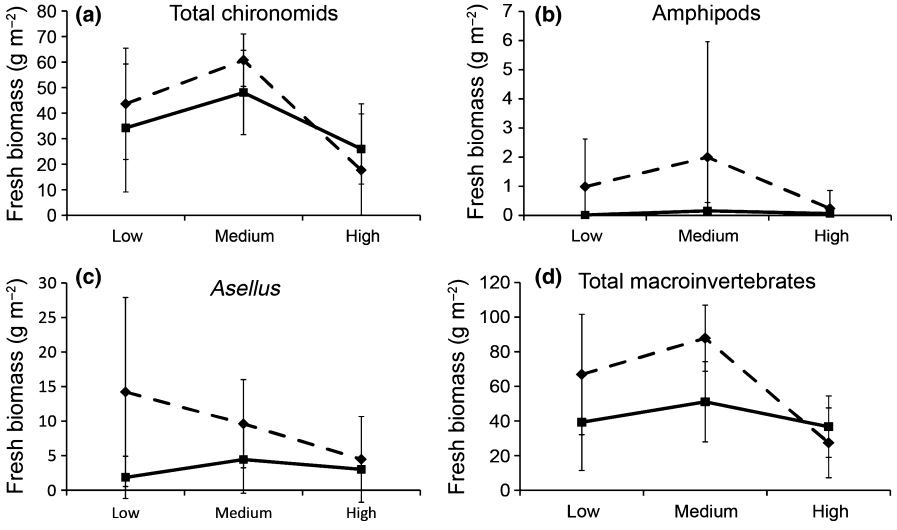

Fig. 4 Interaction effects on sedimentary benthos of Plants × Fish. Data are means with standard deviations for fresh biomass per unit area and are shown for all significant interactions found. Hatched lines are for treatments with no fish and solid lines for treatments with fish. Significant differences were found at low and medium plant densities ($P < 0.05$) but not at high plant densities.

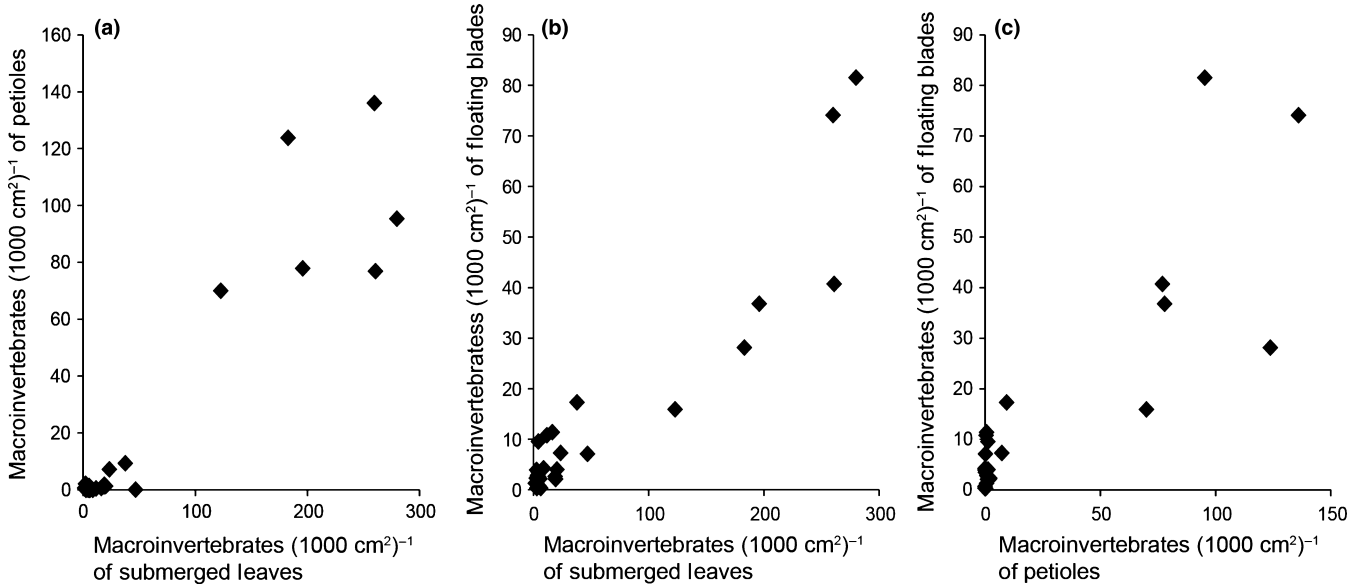

Fig. 5 Scatter diagrams of numbers of macroinvertebrates per unit area of plant surface for combinations of submerged leaves, floating leaf blades and their petioles. Data points are counts for all available shared taxa (total leeches, *Acroloxus lacustris*, *Gyraulus* sp., *Asellus aquaticus* 0–3 mm, *A. aquaticus* 3–6 mm, *A. aquaticus* >6 mm, *Holocentropus picicornis*, total chironomids and total macroinvertebrates, with data for the three different plant treatments individually plotted ($N = 27$ in each plot). r^2 values were 0.9 ($P < 0.0001$) for submerged versus floating leaf blades, 0.53 ($P < 0.0001$) for submerged leaves versus petioles and 0.41 ($P < 0.01$) for petioles versus floating leaf blades.

increasing abundance if habitat (leaf surface) availability were a limiting factor. LAI did not increase with treatment for submerged leaves. Nonetheless, chironomids, *A. aquaticus* and *H. picicornis* did increase on submerged leaves with overall LAI; *Gyraulus* declined; and total macroinvertebrates and *A. lacustris* were unaffected. In contrast, and as expected, on floating leaves and their petioles, total macroinvertebrates and *A. lacustris* did increase with plant treatment, as did total leeches, *H. picicornis* and chironomids. *Asellus aquaticus* was unaffected. The presence or absence of fish (Table 5) had variable effects. Expectation was that fish would reduce the population densities. This was true for submerged leaves for total macroinvertebrates, the leech, *Helobdella stagnalis*, and leeches in general, turbellarians, *A. lacustris* and the larger (but not the smaller) *A. aquaticus*, whilst *Gyraulus*, *H. picicornis* and chironomids increased in the presence of perch. There were fewer effects on the invertebrates of floating leaves with no decreases, increases in *Gyraulus* and chironomids and no significant differences for *A. lacustris* and total macroinvertebrates, which *Acroloxus* dominated. Vulnerability to fish predation thus was generally greater on submerged leaves.

Results of plant treatment on biomass gave broadly similar results (Table S3). On floating leaves and their petioles, biomass either increased significantly or increased without significance being detected, for others. Only for two snails, *Armiger crista* and *Gyraulus*, were there declines and only one of these was significant. Total macroinvertebrates and *A. lacustris* showed strong increases, and significant increases were obtained for some taxa that did not figure when only numbers were considered (notably Turbellaria, leeches, amphipods, Ephemeroptera), whilst *A. aquaticus* did not increase significantly. For submerged leaves, whose LAI did not increase with treatment, there was also a variety of responses as with numbers. Total macroinvertebrates were uninfluenced, nor were *Acroloxus*, *Asellus* or total leeches. But *Erpobdella* sp., *H. stagnalis*, chironomids, and *H. picicornis* showed significant increases, whilst Turbellaria, *A. crista* and *Gyraulus* declined. Where all leaves were combined (Table S3), most taxa tended to increase, *A. aquaticus* was unaffected, and *Gyraulus* declined. The latter two comprised just over a third of the biomass and influenced the results for total biomass, which increased, but significantly only at the 0.1 level.

Parallel patterns on biomass compared with numbers were also obtained for the effects of fish (Table S4). Effects were much stronger, generally leading to decline in the presence of fish, for submerged leaves. Predation was much less influential on the invertebrates of floating leaves and their petioles, and the overall effects were a compromise between effects on submerged and floating leaves. Total numbers, total gastropods, and *A. lacustris*,

Table 2 Effect of plant density on numbers of macroinvertebrates per unit area (1000 cm^2) of different plant surfaces. Only taxa showing significant differences in main effects and other taxa that were particularly abundant are shown

(a) Submerged leaves	Low plant density (N = 12)	Medium plant density (N = 18)	High plant density (N = 18)	P
Total leeches	4.58 ± 3.90 a	1.56 ± 2.01 b	3.89 ± 3.46 ac	**0.025**
Acroloxus lacustris	196 ± 134	183 ± 112	123 ± 58.7	0.15 NS
Gyraulus sp.	37.9 ± 32.1 a	23.6 ± 34.0 ab	19.2 ± 24.2 b	**0.008**
Asellus aquaticus 0–3 mm	4.33 ± 8.48	2.89 ± 3.41	5.22 ± 7.19	0.11 NS
A. aquaticus 3–6 mm	4.33 ± 4.23 a	11.72 ± 11.3 ab	20.3 ± 16.2 a	**0.013**
A. aquaticus >6 mm	3.50 ± 5.20	2.83 ± 5.94	6.33 ± 6.50	0.15 NS
Holocentropus picicornis	8.83 ± 9.97 a	16.4 ± 13.9 a	47.0 ± 45.3 b	**0.001**
Chironomids	2.42 ± 3.78 a	5.67 ± 7.49 a	18.9 ± 21.5 b	**0.006**
Total macroinvertebrates	280 ± 142	260 ± 119	261 ± 106	0.80 NS
(b) Petioles	Low plant density (N = 13)	Medium plant density (N = 18)	High plant density (N = 18)	P
A. aquaticus 0–3 mm	0.15 ± 0.56	0.28 ± 0.67	0	0.24 NS
A. aquaticus 3–6 mm	1.15 ± 1.57	0.44 ± 0.86	1.28 ± 3.32	0.45 NS
A. aquaticus >6 mm	0.69 ± 1.10 a	0 b	0 b	**0.006**
A. lacustris	77.9 ± 28.2 a	123.8 ± 51.3 b	70.0 ± 34.0 a	**0.001**
Gyraulus sp.	9.31 ± 7.80 a	7.22 ± 5.52 a	1.83 ± 2.71 b	**<0.0001**
Total macroinvertebrates	95.3 ± 35.3 a	136 ± 50.6 b	76.9 ± 35.3 a	**<0.0001**
(c) Floating blades	Low plant density (N = 13)	Medium plant density (N = 18)	High plant density (N = 18)	P
A. aquaticus 0–3 mm	3.46 ± 6.94 a	0.33 ± 0.59 b	0.67 ± 1.78 b	**0.028**
A. aquaticus 3–6 mm	9.54 ± 13.0	10.8 ± 16.3	4.00 ± 4.35	NS (0.097)
A. aquaticus >6 mm	2.85 ± 4.08 a	3.89 ± 6.28 a	0.33 ± 0.77 b	**0.038**
H. picicornis	4.23 ± 6.94 a	11.4 ± 8.06 b	7.11 ± 6.83 b	**0.03**
A. lacustris	36.8 ± 38.6	28.1 ± 14.1	15.9 ± 11.1	NS (0.066)
Gyraulus sp.	17.3 ± 12.3 a	7.28 ± 7.92 b	2.11 ± 2.56 c	**<0.0001**
Total macroinvertebrates	81.5 ± 48.0 a	74.1 ± 33.3 a	40.7 ± 18.4 b	**0.002**

Values are means ± standard deviation. Those sharing a letter along rows are not significantly different at $P < 0.05$. Probabilities for non-significant differences that are between 0.051 and 0.1 are shown in parentheses. Values highlighted in bold in this and subsequent tables are significant to at least $P = 0.05$.

Turbellaria and leeches did decline significantly in the presence of perch, but *A. aquaticus*, chironomids and *Gyraulus* did not. This contrasted with vulnerabilities in the sedimentary benthos, where chironomids and especially *Asellus* were reduced in the presence of fish.

There were some interaction effects, which are illustrated in Fig. 6. These effects occurred primarily on submerged leaves. There were few effects for petioles and floating blades, and total macroinvertebrates were uninfluenced. On submerged leaves, interactions between plant and fish treatments suggested that fish predation was ineffective at low and medium plant density for total chironomids and *H. picicornis* but increased their biomass at high plant densities. Patterns were more complex for small *A. aquaticus* and total macroinvertebrates. The former significantly increased with fish at low and high plant densities but decreased at medium plant densities, whilst fish decreased the total biomass of macroinvertebrates at low and medium densities but had no significant effect at high plant density.

Fish diet

Perch ate a variety of food (Table S5) with planktonic cladocerans most common, followed by *A. aquaticus*, various chironomids and *H. picicornis*, in gut contents that contained on average 27.7 items per fish, spread among 23 taxa. There were significant effects of fish on the cladoceran communities, particularly *Daphnia hyalina*, reported in Moss *et al.* (1998). There were significant reductions in numbers of *Asellus* on sediments, owing to fish (Table 1), and in biomass of *Asellus* and chironomids (Table S2), but fish effects were negligible on populations of most of the plant-associated macroinvertebrates that were found as remains in their guts. Calculation of Manly *et al.*'s (1972) index of electivity (Table S5) suggested a strong preference for beetles and

Table 3 Effect of presence or absence of perch on numbers of macroinvertebrates per unit area (1000 cm^2) of different plant surfaces. Only taxa showing significant differences in main effects and other taxa that were particularly abundant are shown

(a) Submerged	No fish (N = 26)	Fish (N = 22)	P (main effect)	P (plants × fish)
Acroloxus lacustris	194 ± 126	129 ± 58	NS (0.074)	0.25 NS
Gyraulis sp.	13.5 ± 14.9	39.8 ± 37.7	**<0.0001**	0.29 NS
A. aquaticus 0–3 mm	2.5 ± 3.15	6.05 ± 8.51	**0.004**	**0.004**
A. aquaticus 3–6 mm	9.46 9.96	17.4 ± 16.1	0.12 NS	**0.012**
A. aquaticus >6 mm	5.38 ± 6.43	3.05 ± 5.53	0.13 NS	0.97 NS
Holocentropus picicornis	14.8 ± 11.8	39.2 ± 44.7	NS (0.055)	**0.007**
Total macroinvertebrates	264 ± 130	267 ± 105	NS	**0.017**
(b) Petioles	No fish (N = 26)	Fish (N = 23)	P (main effect)	P (plants × fish)
A. aquaticus 0–3 mm	0.12 ± 0.43	0.17 ± 0.58	0.24 NS	0.37 NS
A. aquaticus 3–6 mm	0.62 1.06	1.30 3.04	0.23 NS	0.38 NS
A. aquaticus >6 mm	0.35 ± 0.85	0	**0.014**	**0.006**
A. lacustris	85.2 ± 44.7	99.4 ± 48.2	0.25 NS	0.41 NS
Gyraulis sp.	3.12 ± 2.58	8.83 ± 7.64	**<0.0001**	**<0.0001**
Total macroinvertebrates	93.1 ± 46.1	115 ± 40.2	NS (0.055)	0.41 NS
(c) Floating blades	No fish (N = 26)	Fish (N = 23)	P (main effect)	P (plants × fish)
A. aquaticus 0–3 mm	0.85 ± 2.78	1.78 ± 4.85	0.18 NS	0.36 NS
A. aquaticus 3–6 mm	3.12 ± 3.99	13.5 ± 16.0	**0.001**	0.15 NS
A. aquaticus >6 mm	3.46 ± 5.91	1.00 ± 1.54	NS (0.063)	NS (0.068)
Chironomids	1.35 ± 2.10	3.52 ± 2.94	**0.006**	0.98 NS
A. lacustris	28.0 30.1	23.5 ± 13.2	0.58 NS	0.69 NS
Gyraulus sp.	6.04 ± 6.16	10.3 ± 12.7	**0.004**	**0.033**
Total macroinvertebrates	59.8 ± 39.5	68.4 ± 35.6	0.20 NS	0.45 NS

Values are means ± standard deviation. Those sharing a letter along rows are not significantly different at $P < 0.05$. Probabilities for non-significant differences that are between 0.051 and 0.1 are shown in parentheses. Values highlighted in bold in this and subsequent tables are significant to at least $P = 0.05$.

Cricotopus, but these animals were extremely scarce in the environmental samples and these results may be artefactual. More reliable is the relatively strong electivity for planktonic Cladocera and *A. aquaticus* and the discrimination against molluscs.

Calculations of Renkonen indices (Table S5), which attempt to partition feeding among different habitats, are justified because there was strong separation among habitats in their community composition, despite one abundant species (*A. aquaticus*) that was shared. The indices suggest that the perch fed widely among the five possible habitats, with about equal attention to the plankton and the floating leaves. The animals on petioles were avoided, consistent with the results in Table 3, and sedimentary animals were taken more at low plant density than high, consistent with the lower availability (for other reasons, see below) of sedimentary fauna at high plant density. Molluscs, which figured prominently in the plant-associated communities, were barely found in the guts and showed only sporadic effects of fish predation on their numbers.

Discussion

Plant-dominated littoral zones are complex and the simple relationships revealed within plankton communities, where fish have strong effects by removing large, efficiently grazing cladocera, thence favouring rotifers, copepods and small cladocera, should not be expected. The presence of plant refuges for zooplankters in shallow lakes can influence mechanisms in the plankton (Timms & Moss, 1984), and the unexpectedly small effects of fish in determining macroinvertebrate communities in this experiment suggest strong refuge effects for plant-associated organisms also. Although the fish fed on a range of invertebrates and were present at relatively high density, they had impacts on relatively few of the fauna; Diehl (1988), nonetheless, found that perch were superior foragers, compared with bream and roach, among dense vegetation. The strongest effects of perch on the non-planktonic communities in this study were on the sedimentary community below the plants and largely involved the larger motile organisms such as

Table 4 Influence of plant density on density of plant-associated invertebrates for submerged leaves and floating leaves (petioles and blades combined)

(a) Submerged leaves	Low plant density (N = 12)	Medium plant density (N = 18)	High plant density (N = 18)	P
Total leeches	8.50 ± 9.84 a	2.05 ± 2.83 b	6.56 ± 6.11 a	**0.032**
Acroloxus lacustris	324 ± 226	230 ± 169	199 ± 119	0.51 NS
Gyraulus sp.	50.9 ± 30.7 a	22.3 ± 25.3 b	26.3 ± 29.5 bc	**0.007**
Asellus aquaticus 0–3 mm	4.38 ± 7.54	3.91 ± 5.58	7.34 ± 8.38	0.28 NS
A. aquaticus 3–6 mm	7.24 ± 11.1 a	16.8 ± 21.6 ab	29.4 ± 18.7 b	**0.014**
A. aquaticus >6 mm	8.79 ± 17.7	3.33 ± 7.09	9.77 ± 9.88	0.19 NS
Holocentropus picicornis	15.8 ± 18.3 a	21.3 ± 20.7 a	74.7 ± 75.0 b	**0.002**
Chironomids	2.53 ± 4.23 a	7.54 ± 10.7 a	29.6 ± 35.4 b	**0.005**
Total macroinvertebrates	448 ± 259	322 ± 209	404 ± 192	0.48 NS

(b) Floating leaves (with petioles)	Low plant density (N = 15)	Medium plant density (N = 18)	High plant density (N = 18)	P
Total leeches	5.87 ± 8.38 a	5.39 ± 4.68 a	19.1 ± 20.6 b	**0.005**
A. aquaticus 0–3 mm	5.80 ± 9.81	1.78 ± 2.63	4.78 ± 12.9	0.39 NS
A. aquaticus 3–6 mm	15.5 ± 17.4	36.6 ± 56.7	34.6 ± 37.1	0.35 NS
A. aquaticus >6 mm	5.67 ± 8.76	12.4 ± 20.0	2.44 ± 5.63	NS (0.053)
H. picicornis	7.0 ± 12.3 a	35.8 ± 23.9 bc	45.9 ± 40.1 c	**0.001**
Chironomids	6.60 ± 6.32 a	9.33 ± 10.5 a	23.0 ± 22.8 b	**0.004**
A. lacustris	160 ± 74 a	377 ± 122 b	548 ± 288 c	**<0.0001**
Total macroinvertebrates	269 ± 109 a	569 ± 158 b	749 ± 318 c	**<0.0001**

Values are number m^{-2} of bottom habitat and are means ± standard deviation. Values sharing a letter along rows are not significantly different at $P < 0.05$. Probabilities for non-significant differences that are between 0.051 and 0.1 are shown in parentheses. Only taxa showing significant differences and others that were particularly abundant are shown. Values highlighted in bold in this and subsequent tables are significant to at least $P = 0.05$.

A. aquaticus. Burrowing tubificids were relatively immune to predation. Kornijów (1997), however, found some size-selective feeding on the larger chironomids in the surface layers of sediment. The firmly attached *A. lacustris*, which dominated the plant-associated community, was not taken by perch except to a small extent on submerged leaves. In contrast, bluegill sunfish [*Lepomis macrochirus* (Perciformes)] in a Florida lake concentrated more on the epiphytic fauna and took few animals from the benthos (Schramm & Jirka, 1989) but also preferred insects and amphipods. Table 6 summarises the effects of perch. There were 20 instances where perch reduced the numbers of particular taxa, 15 where numbers significantly increased in the presence of perch and 37 where perch had no effect at all. In a broadly similar experiment, Diehl (1992) used the presence or absence of submerged vegetation at three perch densities (0, 2 and 6 fish per 6 m^2) and also found that perch had negligible effects on macroinvertebrate detritivores and herbivores and did not eat molluscs. The perch, however, significantly reduced the numbers of a motile invertebrate predator, *Sialis lutaria*.

Our results are uncomplicated by severe invertebrate predation on the invertebrate communities, as claimed by Sagrario *et al.* (2009) for macrophyte-dominated communities in an Argentinian lake. Their experiments showed that in plastic bags provided with a zooplankton community and three treatments with increasing numbers and diversity of invertebrate predators, there was severe predation on the zooplankters. However, no refuges were provided in the experimental bags, so the results are not representative of conditions in a macrophyte bed. Klecka & Boukal (2014) using laboratory systems with artificial macrophytes showed that structural refuges could have positive or negative effects on the success of invertebrate predators, dependent on the particular predator/prey combination. In streams, Warfe & Barmuta (2004, 2006) found that macrophyte density had little effect on predator success, but that complexity of structure (from *Eleocharis* through *Triglochin* to *Myriophyllum*) did have a major effect with the lesser success in the more complex structure. In our case, however, invertebrate predators were very scarce, probably owing to the low water quality and degree of overnight deoxygenation.

Four specific hypotheses were tested by this experiment. The first was that plant-associated communities are limited by habitat availability so that provision of greater plant biomass would result in larger numbers or biomass per unit area of bottom habitat. This was looked

Table 5 Influence of presence or absence of perch on density of plant-associated invertebrates for submerged leaves and floating leaves (petioles and blades combined)

(a) Submerged leaves	No fish (N = 26)	Fish (N = 22)	P (main effect)	P (plants × fish)
Naididae	0.15 ± 0.77	4.84 ± 5.15	**<0.0001**	0.19 NS
Helobdella sp.	4.69 ± 5.18	0.48 ± 1.13	**0.001**	0.12 NS
Total leeches	8.40 ± 7.63	1.75 ± 3.04	**<0.0001**	0.32 NS
Turbellaria	5.82 ± 8.03	0.61 ± 2.15	**0.005**	0.29 NS
Acroloxus lacustris	321 ± 191	147 ± 80.4	**0.001**	0.18 NS
Gyraulus sp.	24.6 ± 25.6	38.4 ± 33.7	**0.017**	0.9 NS
Asellus aquaticus 0–3 mm	4.38 ± 5.78	6.41 ± 8.68	0.12 NS	**0.009**
A. aquaticus 3–6 mm	17.0 ± 19.8	21.7 ± 20.5	0.87 NS	**0.02**
A. aquaticus >6 mm	10.3 ± 14.4	3.34 ± 5.51	**0.034**	0.75 NS
Holocentropus picicornis	25.9 ± 21.8	56.5 ± 75.1	0.22 NS	**0.017**
Chironomids	9.18 ± 10.4	20.9 ± 35.0	0.31 NS	**0.014**
Total macroinvertebrates	444 ± 224	314 ± 193	**0.026**	**0.026**
(b) Floating leaves (with petioles)	No fish (N = 27)	Fish (N = 24)	P (main)	P (fish × plants)
Total leeches	12.2 ± 17.5	8.25 ± 14.6	0.26 NS	0.55 NS
A. aquaticus 0–3 mm	2.67 ± 6.90	5.54 ± 11.6	0.24 NS	0.65 NS
A. aquaticus 3–6 mm	13.6 ± 17.9	47.8 ± 52.5	**0.005**	0.70 NS
A. aquaticus >6 mm	10.2 ± 17.8	3.21 ± 4.77	**0.05**	**0.047**
H. picicornis	28.8 ± 29.8	33.3 ± 35.4	0.88 NS	0.15 NS
Chironomids	7.78 ± 11.7	19.6 ± 19.3	**0.012**	0.39 NS
A. lacustris	363 ± 266	386 ± 220	0.96 NS	0.48 NS
Gyraulus sp.	24.5 ± 23.3	45.8 ± 34.9	**0.01**	0.56 NS
Total macroinvertebrates	489 ± 300	606 ± 272	0.18 NS	0.42 NS

Values are number m^{-2} of bottom habitat and are means ± standard deviation. Values sharing a letter along rows are not significantly different at $P < 0.05$. Probabilities for non-significant differences that are between 0.051 and 0.1 are shown in parentheses. Only taxa showing significant differences and others that were particularly abundant are shown. Values highlighted in bold in this and subsequent tables are significant to at least $P = 0.05$.

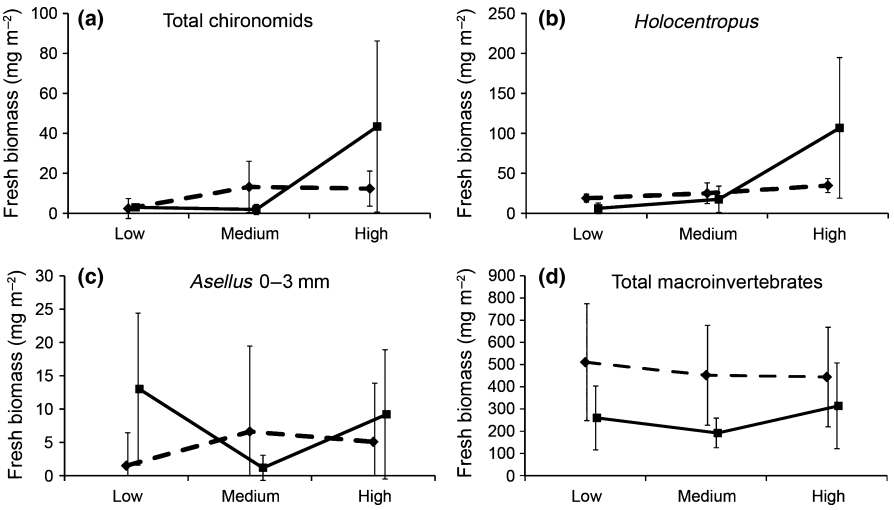

Fig. 6 Interaction effects on biomass of macroinvertebrates on submerged leaves of Plants × Fish. Data are means with standard deviations for submerged leaf area per unit area of bottom. Hatched lines are for treatments with no fish and solid lines for treatments with fish. For (a) and (b), there were significant effects of fish at high plant density but not at medium and low densities. For (c), there were significant effects at all densities and for (d) only at low and medium densities.

at initially on the basis of per unit leaf or petiole area where no significant difference might have been expected and then on the basis of total amount of plant per unit area of bottom where we might have expected a general increase in number of animals. There were unexpected effects on a per unit area of leaf basis (Table 2). *Asellus aquaticus*, *H. picicornis* and chironomids all significantly increased on submerged leaves, with increasing total plant biomass, although these were minority components of a fauna dominated by large

Table 6 Summary of effects of perch. Data are for number of taxa and are taken from original recordings, which have been condensed in previous tables. The effect is to underestimate the numbers of taxa that showed no effect of predation but not to alter the numbers that showed significant effects

	Taxa of actively motile macroinvertebrates			Taxa of macroinvertebrates with no or limited motility		
	Significant reduction with perch	Significant increase with perch	No effect of perch	Significant reduction with perch	Significant increase with perch	No effect of perch
Sediment	3 *Asellus*, Corixidae, Amphipoda	0	2 Ephemeroptera, Coleoptera	2 *Chironomus plumosus*, All chironomids (biomass)	0	9 All chironomids, *C. plumosus* (numbers), *Procladius*, Chironomids other than *C. plumosus*, *Chaoborus*, Trichoptera, *Gyraulus*, *Valvata*, *Helobdella*, Tubificidae
Submerged leaves (leaf area)	1 Turbellaria	0	2 Amphipoda, *Asellus*	2 *Helobdella*, total leeches	2 Naididae, *Gyraulus*	4 *Acroloxus*, *Armiger*, *Holocentropus*, Chironomids
Petioles (leaf area)	1 *Asellus*	0	0	0	1 *Gyraulus*	4 Total leeches, chironomids, *Holocentropus*, *Acroloxus*
Floating leaves (leaf area)	0	0	0	0	2 Chironomids, *Gyraulus*	3 Total leeches, *Holocentropus*, *Acroloxus*
Submerged leaves (bottom area)	2 Turbellaria, *Asellus*	0	1 Amphipods	3 *Helobdella*, total leeches, *Acroloxus*	2 Naididae, *Gyraulus*	2 *Armiger*, *Holocentropus*, Chironomids
Petioles (bottom area)	1 *Asellus*	0	0	0	1 *Gyraulus*	4 Total leeches, chironomids, *Holocentropus*, *Acroloxus*
Floating leaves (bottom area)	0	1 *Asellus*	0	0	2 Chironomids, *Gyraulus*	3 Total leeches, *Holocentropus*, *Acroloxus*
All vegetation (bottom area)	2 Turbellaria *Asellus* (>6 mm)	1 *Asellus* (3–6 mm)	1 Amphipods	3 *Helobdella*, Total leeches, *Acroloxus*	3 Naididae, Chironomids, *Gyraulus*	2 *Holocentropus*, *Armiger*

numbers of *A. lacustris*. Total submerged leaf area did not change with increase in total plant biomass. This result might be explained by reduced light, hampering the visually feeding perch, at the surfaces of the submerged leaves, with increased leaf canopy. On petioles of floating leaves, there was no prominent pattern in numbers per unit area, although some statistical significance was shown and total macroinvertebrates per unit leaf area of floating blades decreased with increase in total vegetation. This was influenced by a decline, which was by itself not significant, in *A. lacustris* and might be artefactual.

The hypothesis concerned total provision of leaf surface, however, and the key data are in Table 4 for floating leaves with their petioles, which dominated the vegetation, and showed increases in numbers of *Acroloxus lacustris*, *Holocentropus picicornis*, chironomids and total macroinvertebrates. Parallel data are shown in Table S3 for the entire vegetation and invertebrate biomass, where increases were seen for most macroinvertebrates, though not all differences, including total macroinvertebrates, were significant . A simple pattern was disturbed by peaks in abundance at medium plant density for two snail taxa. Overall, however, it would be fair to say that more vegetation generally did mean more macroinvertebrates per unit area of lake and therefore that availability of habitat space could be a limiting factor for the animal community. This is a more subtle conclusion than that of Diehl (1992) who found, perhaps inevitably, that macroinvertebrate numbers increased in the presence of submerged vegetation (charophytes, elodeids, pondweeds) compared with the absence of it.

The different parts of the plants were influential in determining both communities and density of animals per unit area of plant, the second hypothesis proposed. Floating leaves and their petioles are more rigid, are covered by a thicker cuticle and rise higher in the water column than submerged leaves, which, like submerged vegetation in general, are thinner, more flexible and perhaps more easily colonised by periphyton on account of their less waxy surfaces. Submerged leaves also occurred on short petioles close to the bottom and therefore in lower light intensities. Densities of animals were greater on submerged leaves than on floating leaves or (their fully submerged) petioles by factors of 2 and 2.6, respectively. Petioles were apparently over three times more attractive

than the floating blades to which they were attached; predation effects were very small on both petioles and blades of floating leaves compared with submerged leaves (Table 3). Van de Meutter, Cottenie & De Meester (2008) examined a range of plant structures and found that macroinvertebrate abundance and richness were least on floating-leaved *Nuphar* compared with submerged species (*Potamogeton*, *Utricularia*) and even the submerged parts of emergents such as *Phragmites* and *Typha*, although plant structure explained only 21% of the variance in the data. Walker, Wijnhoven & van der Velde (2013) reiterate the long-held understanding that finely divided submerged leaves support richer invertebrate communities than undivided ones. Cheruvelal *et al.* (2002) found likewise in mid-western North American lakes, Thomaz *et al.* (2008) in a Brazilian floodplain and Taniguchi, Nakano & Tokeshi (2003) and Ferreiro *et al.* (2014) for stream macrophytes and plastic versions of them.

The greater densities of animals per unit leaf area on submerged leaves compared with floating ones could have been due to reduced intensity of predation in a darker environment (see above) (Diehl, 1988; Nurminen, Pekcan-Hekim & Horppila, 2010a; Nurminen *et al.*, 2010b). It is also possible that a greater natural turnover of floating leaves (which are more easily damaged mechanically or by leaf miners) (Brock & van der Velde, 1996; Cronin *et al.*, 1998; Kornijów & Ścibior, 1999; Cronin, Lewis & Schieser, 2006) may have discouraged colonisation. There was turnover in the floating leaf population during the experiment, and numbers were maintained by selecting new leaves to replace those that had died. Consistent with this is that petioles (with higher densities of animals) are longer-lived than the floating blades, which only fully expand when they reach the surface. The periphyton food source on submerged leaves was likely to have been lower in the presence of fish than in their absence because fish caused a threefold increase in overlying phytoplankton chlorophyll (Moss *et al.*, 1998). There was also a decline in submerged leaf area in the presence of fish. This could not have been due to the removal of specialist leaf grazers (Cronin *et al.*, 1998, 2006), none of which were noted, but was more likely due to the increased shading that resulted from a higher phytoplankton chlorophyll a concentration consequent on the removal of large cladocerans by the fish. Nonetheless, despite potential indirect and direct effects of fish through reduced light and predation, respectively, there were similar total macroinvertebrate population densities on the submerged leaves compared with the control. This suggests powerful compensatory mechanisms, yet undefined, but perhaps involving selective removal of invertebrate predators such as leeches, turbellarians and corixids, stabilising the invertebrate populations.

The third hypothesis proposed that the generalist fish predator used would show selective predation resulting in reduction in numbers of motile, more easily detectable animals, such as crustacea and predatory insects, compared with sedimentary or slow-moving ones, including gastropods and case builders. Table 6 shows that this hypothesis was supported. Of 20 instances where perch reduced numbers, only half involved highly motile animals, but when data are expressed as percentages of total possible instances, this was 67% for highly motile animals but only 18.5% for less motile and sedentary animals. The implications are that moving animals may attract the attention of the fish much more easily than the sedentary ones, despite the fact that immobility would seem to suggest greater vulnerability. Perch are active feeders, attracted also by zooplankton, which were the major components of their diet (Table S5). After these, *A. aquaticus* was the second most common item in fish guts. Feeding on burrowing invertebrates additionally requires techniques that are non-visual such as the lateral line in fish (Helfman *et al.*, 2009; Schwalbe, Bassett & Webb, 2012). Other taxa, including amphibians, also use sensitive lateral line organs to locate prey and indeed may demonstrate size-selective feeding when they do so (Measey, 1998).

There were rather more instances of plant-associated taxa increasing rather than decreasing in the presence of fish (Table 6), a phenomenon also described, but unexplained, by Ferreiro *et al.* (2014) in *Egeria* beds in a South American stream. The reasons for this are obscure but might include the removal of large invertebrate predators by fish, although this is unlikely in our system, or the removal of competitors for periphyton food.

Fourthly, we hypothesised that greater provision of macrophyte biomass would result in greater numbers and biomass of sedimentary benthic invertebrates through greater supply of organic matter to the bottom, as suggested in other studies (Brock & van der Velde, 1996; Żbikowski *et al.*, 2010). This was not supported. With increasing density of vegetation, the sedimentary benthos became scarcer in numbers and this was consistently so for all but tubificids. The reasons are not clear. One possibility is that greater shading by overlying vegetation reduced the production of surface sediment algae, on which many of the benthic feeders may depend. Hansson (1992) found the major limiting factor to growth of algae on bottom sediments to be light. This may also have been a component in reduction of the

benthic animal community in the presence of fish, which, through their feeding on *Daphnia* in particular (Moss *et al*., 1998), allowed a greater build-up of chlorophyll and hence shading effects of planktonic algae. Tubificids, feeding at depth in the sediment rather than at the surface like most of the other benthic animals, would have been less influenced by this, although the larger instars also collect algae from the surface sediment. Algal material is in general of higher food quality than residual organic matter, and influences of it may have been greater than proportional.

Finally, our design allowed us to look at interactions between plant density and fish treatments and we hypothesised that fish predation might be hampered at high densities of plants. We found relatively few interactions but most supported the hypothesis. Fish fed less effectively in the high-density plant treatment than in the medium- and low-density treatments, and most effects involved the sedimentary benthos, with a few for the submerged leaves and very few for the floating blades or petioles. The reasons why fish effects were lesser at high plant density might be because of greater impedance, especially by the clutter of petioles, in fish getting to the sediments (and also to the submerged leaves), but also because potential shading effects of the plant biomass may have reduced the numbers of favoured prey such as the detritivore/herbivore *A. aquaticus*, through reduction in sedimentary algal food. Plant structures clearly provide refuges and it follows that the denser the structure, the greater the refuge, although there can be complications not only from the specific predators and prey but also because of greater provision of food within the plant beds. Scheinin *et al*. (2011) caution against the use of simplified designs in laboratory experiments compared with natural situations in investigating these issues.

Two major conclusions emerge from this work. Firstly, the littoral zone macroinvertebrate communities are poorly characterised in studies that use gross sweep or grab samples. There are differences between the underlying sediment and the plants (Table S1), even if some taxa, such as *A. aquaticus*, are shared between them, and even among the components of a single plant species, notably the distinctions between submerged and floating leaf blades, but also between the leaf blades and their petioles. The predominance of *A. lacustris* on petioles, for example, was associated with reduced use by fish of petiole macroinvertebrates, compared with those on leaf blades (Table 6). Only one fish species could be used because of availability and the size of the enclosures. A mixed fish community including species such as tench, which tends to favour gastropods and other plant-associated taxa, would add even greater complexity, and indeed, there is a large literature documenting the defining of different feeding niches by mixed fish communities (e.g. Werner *et al*., 1983; Hanson & Leggett, 1986; Mittelbach, 1988; Dieterich, Baumgartner & Eckmann, 2004; Rezsu & Specziar, 2006; Estlander *et al*., 2010; Dukowska *et al*., 2012; Dukowska & Grzybkowska, 2014).

Secondly, even given the limitations of the fish used, there was a much lesser effect of fish predation on the plant-associated and benthic communities than expected. Diehl (1993), Thorp & Bergey (1981a,b), Bronmark (1994) and Kornijów *et al*. (2005) concur in this. Nurminen, Horppila & Peckan-Hekim (2007) found that association with shaded leaf surfaces in daylight greatly reduced fish predation on the large cladoceran, *Sida crystallina*. Bronmark (1994) used both the specialist tench, and perch in vegetated enclosures and found the effects of tench on snail populations, but few effects of perch. Crowder & Cooper (1982) suggest that dense macrophyte structures inhibit foraging and allow even abundant, highly profitable prey to coexist with predators. They found that bluegill sunfish, feeding in high macrophyte densities, ate fewer but large prey and had a narrower diet than expected. Likewise, Savino & Stein (1982) noted that predation of largemouth bass (*Micropterus salmoides*) on bluegill sunfish was greatly inhibited when the density of (artificial) plant stems was increased from 50 to 1000 stems m^{-2}. In contrast, at least during the first year after their introduction to a small Canadian lake, yellow perch (*Perca flavescens*) reduced benthic invertebrate biomass by 60% (Post & Cucin, 1984). But in experiments with fish and turtle-proof cages in a reservoir with a soft bottom, Thorp & Bergey (1981a,b) found little effect of vertebrate predation on the bottom communities, whilst Harrison, Bradley & Harris (2005) found that macrophyte refuges allowed coexistence of amphipods and bullhead (*Cottus gobio*) in streams through differential movements of predator and prey between the plant beds and the mid-stream areas.

The large literature showing how fish severely manipulate zooplankton communities creates an expectation that the same must be true of the benthic and epiphytic littoral invertebrate communities, but this was not so. The greatest predation effects in this experiment were on the plankton and then on the motile sedimentary benthos, particularly *A. aquaticus*, which might be perceived to have similar traits as the planktonic cladoceran most favoured by the fish (Fig. 7). Again a more complex picture would emerge with a mixed fish community, but the Renkonen indices calculated suggest that the perch

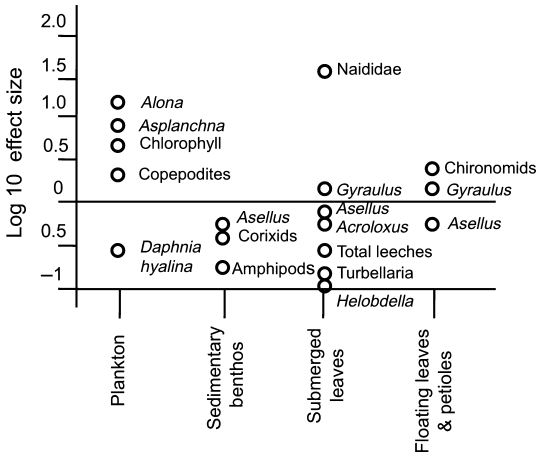

Fig. 7 Relative effect sizes of fish on planktonic, sedimentary benthic and plant-associated communities. Effect sizes were calculated as the ratio of numbers in the presence (a) compared with the absence (b) of fish. All values are per m^2 of lake bottom. Data for plankters are taken from Moss *et al.* (1998).

were feeding actively in all habitats. This work thus supports the idea that littoral plant-dominated communities have strong buffer mechanisms that allow periphyton grazers to persist even when pressed by drivers such as fish predation. The lily beds in Little Mere persisted even when there was very large loading from sewage effluent discharged directly into the mere prior to 1991 (Moss *et al.*, 2005). The persistence of such plant communities must arise from a large range of mechanisms that can only be revealed in full by many more experiments such as this one but using different fish and other impacts as experimental drivers.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Densities (means in August over all treatments) for full list of benthic invertebrates (per m^2 of bottom) and plant-associated invertebrates (per 1000 cm^2 of leaf surface).

Table S2. Influence of overlying lily density, presence or absence of perch and time on biomass of sediment benthos.

Table S3. Influence of plant density on biomass of plant-associated invertebrates for submerged leaves and floating leaves (petioles and blades combined).

Table S4. Influence of presence or absence of perch on biomass of plant-associated invertebrates for submerged leaves and floating leaves (petioles and blades combined).

Table S5. Prey selectivity, Manly and Renkonen Indices.

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